

Adult proximity and frugivore's activity structure the spatial pattern in an endangered plant

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Summary

1. Seed dispersers play a key role in shaping the spatial patterns of plant populations. After their disappearance, we expect a substantial increase in plant aggregation, which can ultimately cascade into high plant competition.

2. We used data of fully mapped distribution of four populations of the shrub *Daphne rodriquezii* from Menorca Island (Balearic Islands, W Mediterranean Sea), one in which *D. rodriquezii* coexists with its only disperser, the lizard *Podarcis lilfordi*, and three populations where this lizard went extinct long ago.

3. We used spatial point-pattern analysis to better understand the lizard's role on the spatial distribution of *D. rodriquezii*. To this end, we used specific point-process models that represented our main hypotheses on the impact of (i) habitat suitability, (ii) disperser activity, (iii) proximity of adults on the distribution of juvenile and adult shrubs and (iv) the impact of adult proximity on juvenile survival.

4. Plants were aggregated in all populations, and aggregation at short distances was stronger in populations without lizards. The observed spatial pattern of juveniles was better explained by a combination of hypotheses (ii) and (iii). The density of juveniles below adults was similar in all populations, but density far from adults was higher in the population with dispersers. In populations without dispersers, juveniles suffered higher mortality below adults.

5. Overall, our results suggest that the effects of lizard extinction were subtle. In the absence of lizards' dispersal, plants self-replace in favourable locations, but a decline in density, is evidenced near adults attributed to higher competition. Lizards, which often defecate under fruiting plants, create also a tight juvenile–adult association, but allow juveniles to escape from the immediate proximity of adults attributed to longer-distance movements. Our study shows how the analysis of the spatial pattern of plants can lead to detailed hypotheses on the underlying mechanisms structuring plant populations.

Key-words: habitat suitability, heterogeneous Poisson process, point-pattern analysis, seed dispersal, spatial distribution, univariate and bivariate cluster process

Introduction

Clustering of individuals is common in plant populations (He, Legendre & LaFrankie 1997; Condit *et al.* 2000; Wiegand *et al.* 2007). Because plants respond primarily to the biotic and abiotic conditions within their immediate neighbourhood (Purves & Law 2002), the processes that affect

their spatial distribution would affect subsequent demographic processes (Getzin *et al.* 2008). Seeds are the only dispersive life stage and, therefore, seed dispersal often contributes to spatial patterning in adults (Seidler & Plotkin 2006; Muller-Landau *et al.* 2008; Wiegand, Martínez & Huth 2009). In animal-dispersed plant species, the activity of frugivores can leave signatures in the distribution of recruits encompassing different spatial scales (Howe 1989; Russo & Augspurger 2004; Rodríguez-Pérez, Wiegand & Santamaría 2012).

Limited dispersal can cause strong spatial aggregation of seeds and tight association with adults, thereby creating

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spatial patterns that can persist well beyond the seedling stage (Condit *et al.* 2000; Levine & Murrell 2003; Cramer *et al.* 2007). It is also acknowledged that the processes occurring subsequent to seed dispersal can alter or blur the initial seed-distribution template. For instance, spatial aggregation induced by limited dispersal could be reinforced by a patchy distribution of suitable habitat (Webb & Peart 2000) as recruits are thought to be especially sensitive to the availability of suitable microsites (e.g. regeneration niches; Grubb 1977). Proximity of adults may also lead to competition and density-dependent mortality that reduces the degree of aggregation in seedlings (Harper 1977).

A fundamental but difficult task in research on plant–frugivore interactions is to explore the dispersers' role in shaping the spatial patterns of the plant in the long term. The short-term effects of the frugivore on seed dispersal or recruitment can be studied by exclusion experiments (e.g. Traveset & Riera 2005; Rodríguez-Pérez & Traveset 2010), but the cumulative long-term effects that arise from the feedbacks of demographic processes with (or without) seed dispersal service cannot be studied by normal exclusion experiments because the past effects of the dispersers will be visible for several plant generations. One must therefore rely on rare cases of 'historical' exclusions (e.g. Traveset & Riera 2005; Anderson *et al.* 2011). One such exceptional case is the mutualistic plant–animal system between of the threatened plant *Daphne rodriguezii* T. (Thymelaeaceae) and its unique seed disperser, the endemic Balearic lizard, *Podarcis lilfordi* G. (Lacertidae) which is locally extinct at several *D. rodriguezii* populations but still persists in one (Traveset & Riera 2005). One approach to advance our understanding of plant–frugivore interactions is to conduct a detailed analysis of the observed spatial patterns (Wiegand, Martínez & Huth 2009). Spatial patterning may conserve an imprint of past processes constituting an 'ecological archive' from which we may recover information on the underlying processes (Wiegand *et al.* 2003; Law *et al.* 2009; McIntire & Fajardo 2009).

In this study, we applied spatial point-pattern analysis (Wiegand & Moloney 2004; Perry, Miller & Enright 2006; Law *et al.* 2009) to characterize the spatial patterns of four fully mapped populations of *D. rodriguezii* – one in which its lizard disperser remains and three without its disperser. Our goal is to understand how the extinction of an important disperser has affected the spatial distribution of *D. rodriguezii*. Here, we derived specific point-process models that represented our main hypotheses on the impact of (i) habitat suitability, (ii) disperser activity and (iii) proximity of adults on the spatial patterns of juvenile and adult shrubs, and we investigated the impact of adult proximity on juvenile survival. We used the software PROGRAMITA (Wiegand & Moloney 2004) to generate multiple point patterns of each point-process model and compared them with the observed point patterns.

On the basis of prior knowledge of this system, we expected limited dispersal around adult plants to produce

a high degree of clustering in the absence of the disperser (Traveset & Riera 2005). Previous experimental studies on *D. rodriguezii* showed that the abundance and survival of seedlings strongly depended on the presence of nurse plants (Traveset & Riera 2005; Rodríguez-Pérez & Traveset 2010), which indicates that habitat suitability is a key process of its population dynamics (Rodríguez-Pérez & Traveset 2012). Conversely, in the population where plants and lizards coexist, we thus expected that the spatial pattern of plants to primarily depends on disperser activity and plant habitat preferences, and less on the adult template (Rodríguez-Pérez, Wiegand & Santamaría 2012). Finally, dispersal limitation should increase local plant density and, hence, we would expect a signal of competition and density-dependent mortality in populations without lizards.

Material and methods

STUDY SPECIES

Daphne rodriguezii Teixidor (Thymelaeaceae) is a small evergreen shrub (up to 1.5 m in height), endemic to Menorca Island (Balearic Islands, W Mediterranean Sea). It inhabits the coastal shrubland and is highly associated with shrub patches of *Phillyrea latifolia*, *Pistacia lentiscus* and *Erica multiflora*. It is scattered along the NE coastline of the island, in populations ranging in size from several dozen to <300 individuals. By far, the largest population is found on Colom Islet (up to 18 000 individuals, and located in an islet of c. 60 ha. at c. 200 m east of Menorca), where this species coexists with its only seed disperser, the endemic lizard *P. lilfordi* (Traveset & Riera 2005). Its fruits (orange-red drupes) develop in May–June and are quickly and completely consumed by *P. lilfordi*. Fruits fall passively under adults in populations without dispersers (Traveset & Riera 2005). There is no evidence that other frugivores consume *D. rodriguezii* fruits (Traveset & Riera 2005; Rodríguez-Pérez & Traveset 2010).

STUDY SITES AND SAMPLING

For this study, we mapped all juvenile and adult *D. rodriguezii* plants in three study plots at Menorca Island (Mesquida, Favàritx and Pudent) that encompass the entire populations (Fig. 1). The extinction of *P. lilfordi* occurred in Menorca probably ca. 2000 years ago (Reumer & Sanders 1984). It is therefore unlikely that past interactions with lizards shaped the current spatial distribution of *D. rodriguezii*. The plot in Colom Islet where the lizard is still present included only a fraction of a large *D. rodriguezii* population. More details about these plots can be found elsewhere (Traveset & Riera 2005; Rodríguez-Pérez & Traveset 2010, 2012).

We carried out plant surveys during the period 10–20 May 2008. We mapped all individual plants within the study plots with a hand-held submeter GPS (Trimble GeoXT) that achieves c. 50-cm accuracy for GPS code measurements after post-processing. Furthermore, we also took plant size measures (height and maximum crown diameter, ± 1 cm) and calculated the volume of the cylinder enclosing each individual plant. Finally, we classified each plant as adult or juvenile based on a size threshold (i.e. adults were those larger than 2×10^3 cm³; Rodríguez-Pérez & Traveset 2012).

During the last 10 years, we intensively monitored all plots without dispersers, recording the individual mortality (Fig. 1). Because the number of living juveniles was very low during some

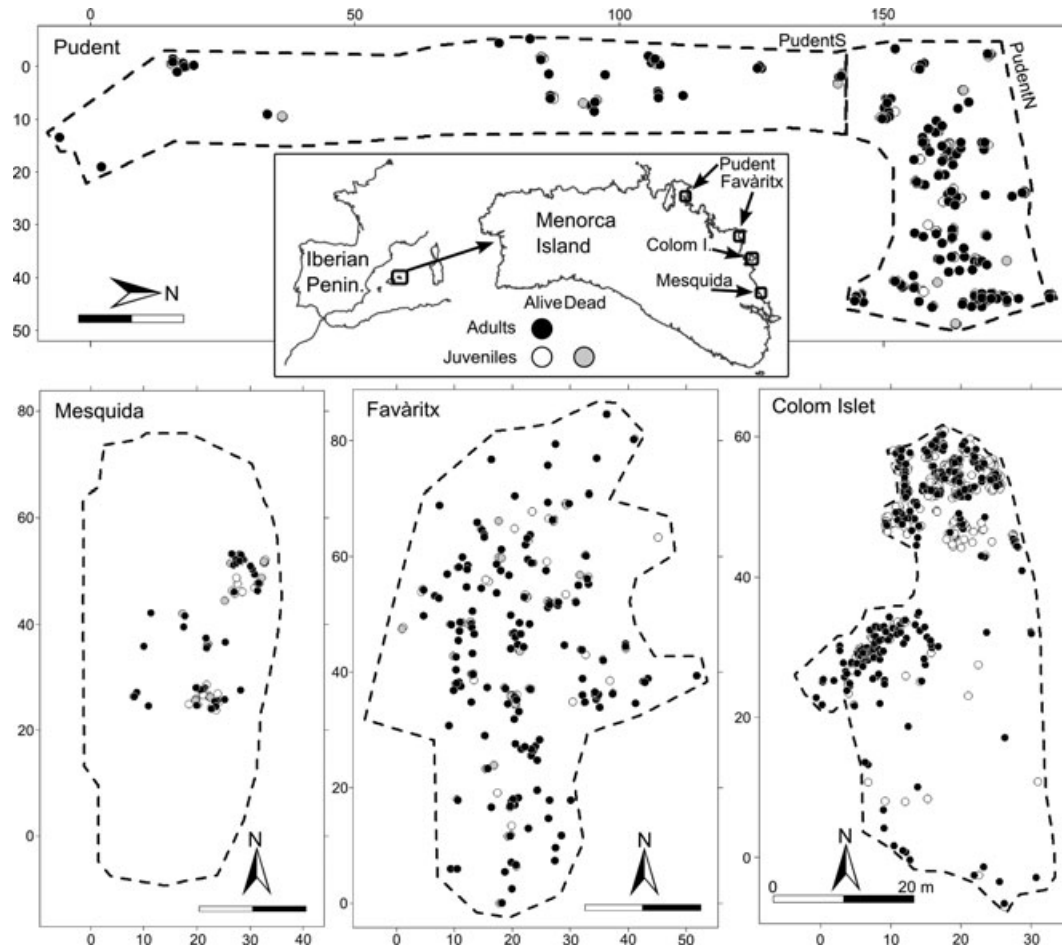


Fig. 1. Location of the *Daphne rodriguezii* populations at Menorca Island and the spatial distribution of adults (black circles), alive (open circles) and dead juveniles (grey circles) within each plot. The limit of each plot is shown as dash lines. We subdivided the Pudent plot into PudentN and PudentS (see Appendix S1, Supporting information). The numbers of adults and juveniles plants were Mesquida (44, 9), Favàritx (145, 42), PudentS (34, 23), PudentN (118, 119) and Colom Islet (262, 203).

years, we analysed only the mortality of juveniles during the last 5 years, pooling all dead and alive plants independently of the year of mortality. In Colom Islet, we did not monitor survival for logistic reasons.

GENERALITIES OF SPATIAL ANALYSIS

We used techniques of spatial point-pattern analysis (Wiegand & Moloney 2004; Law *et al.* 2009) to describe the spatial patterns of juvenile and adult *D. rodriguezii* plants, the juvenile–adult association and juvenile survival in respect to proximity of adults. To capture the statistical properties of the point patterns (Diggle 2003; Illian *et al.* 2008), we used summary statistics such as the pair-correlation function and the distribution function of the distances to the nearest neighbour. To test our ecological hypotheses on the impact of habitat suitability, disperser activity and proximity of adults on the spatial patterns of juvenile and adult shrubs, we implemented specific point-process models that represent our ecological hypotheses (Wiegand & Moloney 2004; Jacquemyn *et al.* 2007). We then calculated summary statistics for the observed pattern and the pattern arising from multiple (199) simulations of the point-process models. We used the latter simulations to estimate the envelopes that encircle the 95% range of values of the summary statistic under a given point-process

model (i.e. the 5th lowest and highest values). Departures from the point-process models occurred if the observed summary statistics were outside the simulation envelopes (Wiegand & Moloney 2004).

SUMMARY STATISTICS OF SPATIAL POINT STRUCTURES

The neighbourhood-density function $O(r)$ is the average density of point at distance r from the points of the pattern. Comparison with the overall point density λ intensity (i.e. total number of points divided by area) reveals basic properties of the pattern. Random patterns yield $O(r) = \lambda$, aggregated patterns with locally elevated neighbourhood densities yield $O(r) > \lambda$ and regular patterns $O(r) < \lambda$ (Wiegand & Moloney 2004). Extensions for bivariate patterns composed of two types of points follow intuitively and the $O_{12}(r)$ estimates, for instance, the mean density of juveniles (subscript 2) at distance r of adults (subscript 1). To compare patterns with different overall density λ , the pair-correlation function $g(r)$ is used. It is obtained by normalizing with the intensity: $g(r) = O(r)/\lambda$ and $g_{12}(r) = O_{12}(r)/\lambda_2$. The cumulative distribution function $D(r)$ of the distances r to the nearest neighbour provides additional information (Illian *et al.* 2008) and is used to test the fitted point-process models.

We used the software PROGRAMITA (Wiegand & Moloney 2004) for all point-pattern analyses. We restricted our analyses to the irregularly shaped areas of the sampled plots (see Fig. 1) and subdivided the study site Pudent into the two internally homogeneous plots PudentS and PudentN (Appendix S1, Supporting information; Péliissier & Goreaud 2001). Because we expected similar ecological conditions among the plots without disperser, we combined the results of the individual analyses using techniques for replicated patterns (i.e. Illian *et al.* 2008; Raventós, Wiegand & Luis 2010).

ANALYSIS 1: DIFFERENCES IN SPATIAL PATTERNS IN PLOTS WITH AND WITHOUT DISPERSER

To reveal detailed cluster properties of the observed patterns, we compared them to 'benchmark' processes that describe basic features of clustering (e.g. Wiegand *et al.* 2003; Jacquemyn *et al.* 2007; Law *et al.* 2009; Wiegand, Martínez & Huth 2009). The objective here is not to find a point process that fits best, but to interpret departures from the benchmark to better describe the patterns.

Because most univariate patterns were clustered (Fig. 1), we contrasted the spatial patterns of juvenile and adult to homogeneous Thomas processes (Wiegand, Martínez & Huth 2009). Thomas processes describes clustering in a simple way and can be easily fitted to a pattern because their pair-correlation function can be expressed in a closed form. A realization of a Thomas process with n points comprises c randomly located clusters; the number of points per cluster follows a Poisson distribution with mean μ , and points of the cluster are distributed with a Gaussian kernel function with variance σ^2 centred at the cluster centre. Thus, 2σ can be interpreted as cluster size because 95% of all points of a cluster are located within distance 2σ of the cluster centre. Consequently, the pair-correlation function will have values larger than one for distances smaller than 4σ . Clustering increases if the number of clusters decreases and if the cluster size decreases. Technical details can be found in Wiegand, Martínez & Huth (2009) and Appendix S1 (Supporting information).

ANALYSIS 2: RELATIVE IMPORTANCE OF DIFFERENT PROCESSES

We formulated specific point-process models that represent different hypotheses on the factors that may influence the spatial distribution of *D. rodriguezii* plants. For detail on the different point-process models, see Appendix S2 (Supporting information).

Habitat suitability, hypothesis (i)

To implement the habitat hypothesis for juveniles and adults, we randomly redistributed the observed *D. rodriguezii* plants, following previously developed habitat suitability maps (Rodríguez-Pérez, Wiegand & Santamaría 2012; Appendix S1, Supporting information). To this end, we generated random locations within the study area and retained a point proportionally to the habitat suitability at this location. As a result, the local plant density will be proportional to the habitat suitability.

Seed disperser activity, hypothesis (ii)

To implement the seed disperser hypotheses for juveniles and adults, we used habitat suitability maps for lizards' home ranges derived in Rodríguez-Pérez, Wiegand & Santamaría (2012;

Appendix S1, Supporting information). The corresponding point-process model was analogous to that of the habitat hypothesis and generated patterns with local plant densities proportional to the disperser's habitat use.

Dependence on adults, hypothesis (iii)

Here we assumed that the juvenile distribution depended directly on the adults' pattern (Jacquemyn *et al.* 2007). In the corresponding point-process model, the locations of juveniles are governed by a kernel function centred in the observed locations of the adult plants. We used a two-dimensional normal distribution with variance σ^2 as kernel (Jacquemyn *et al.* 2007). Superposition of the kernel functions yields a map proportionally to the expected juvenile density that is used as above to generate patterns where the density of juvenile depends on the distance from adults. We systematically varied the value of the unknown parameter σ and searched the value that produced a reasonable fit.

Combined hypotheses

Because all three point processes use the same framework of probability maps (i.e. heterogeneous Poisson processes; Wiegand & Moloney 2004), we contrasted the plant distributions also to point-process models based on the combined probabilities of habitat suitability for plants, disperser and the seed shadows.

ANALYSIS 3: MORTALITY IN PLOTS WITHOUT DISPERSER

In this analysis, we quantified the impact of adults on juvenile survival, that is, we tested whether the probability of juvenile mortality depended on the distance r to adults. The appropriate summary statistic for this question is the probability $p_{a,2}(r)$ that a juvenile (coded with subscript 2) at distance r from an adult (coded with subscript a) survived. We tested our hypothesis by contrasting the observed pattern to a point-process model representing random mortality of juveniles (Raventós, Wiegand & Luis 2010). In this null model, the observed label 'dead' of juveniles is randomly shuffled among juveniles.

Results

ANALYSIS 1: DIFFERENCES IN SPATIAL PATTERNS IN PLOTS WITH AND WITHOUT DISPERSER

The three plots without disperser contained 339 adults. The pair-correlation function $g(r)$ indicated that the local neighbourhood density was more than 10 times higher than expected by a random distribution (Fig. 2a) and that the strong clustering disappeared at distances >4.0 m [i.e. the $g(r)$ approached at 4 m the expectation for random patterns]. Fitting Thomas processes yielded a cluster size of c . 2.2 m in all plots without disperser (see Fig. S6, Supporting information). This suggests that the same underlying mechanisms were acting in these plots. Realizations of the fitted Thomas processes approximated the observed $g(r)$ reasonably well (Fig. 2a), but somewhat underestimated the neighbourhood density at larger distances. Testing the fitted point-process model with the nearest-neighbour distribution function $D(r)$ supported this finding (inset

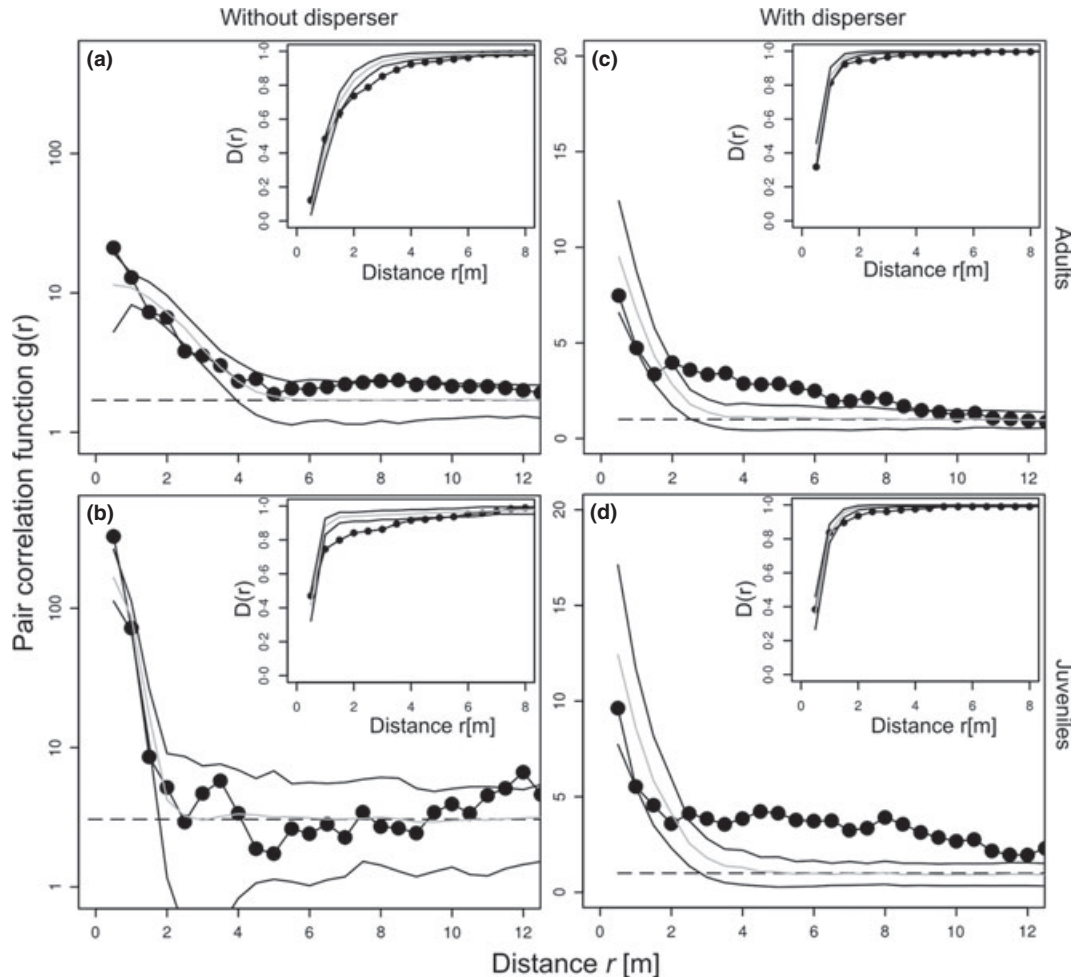


Fig. 2. Analyses of clustering of adult (upper panels) and juvenile *Daphne rodriguezii* plants (lower panels) in the plots without (left) and with disperser (right) disperser. The results of the three plots without disperser are averaged (Fig. S6, Supporting information shows results for individual plots). The pair-correlation functions estimated from the data (lines with dots) is contrasted to simulations envelopes (black lines) derived from the 199 realizations of the fitted Thomas processes. The expectation under the null model is shown as grey line and that of random patterns as dashed line. The small insets show the analogous results for empirical distribution function $D(r)$ of the nearest-neighbour distances which we did not used for fitting.

Fig. 2a); however, the smaller departures from the observed $D(r)$ indicated some ‘isolated’ adults with less neighbours than expected by this point process.

The juveniles ($n = 189$) in plots without dispersers were highly clustered; the $g(r)$ indicated that their local neighbourhood density was *c.* 20–120 times higher than expected by a random pattern and that the strong clustering disappeared rapidly at distances >1.5 m (Fig. 2b). For all three plots, a cluster size of $2\sigma = 1.4$ m provided a good fit (Figs 2b and S6, Supporting information). Test with $D(r)$ indicated that *c.* 10% of the juveniles had their nearest neighbour further away than expected by the Thomas process (inset Fig. 2b).

The patterns in the plot with disperser were different from that without disperser. Adults ($n = 261$) and juveniles ($n = 203$) formed basically two dense clusters and *c.* 6% isolated individuals (Fig. 1; 18 adults and nine juveniles were located outside the clusters). Fitting Thomas processes to the data indicated for both adults and

juveniles a clear signal of small-scale clustering (Fig. 2c, d; $2\sigma = 2.1$ and 2.3 m, for adults and juveniles, respectively). However, the neighbourhood densities at distances of 2–12 m were substantially larger than expected (Fig. 2c, d).

ANALYSIS 2: RELATIVE CONTRIBUTION OF DIFFERENT PROCESSES

Habitat and disperser activity

The point processes based on the habitat hypothesis and the seed disperser activity hypothesis clearly failed to capture the observed small-scale clustering at distances smaller than 4 m; the observed $g(r)$ was clearly outside the simulation envelopes (Figs S7 and S8, Supporting information) and somewhat surprisingly, did not fit at larger distances better than the Thomas (Figs 2, S7 and S8, Supporting information).

Dependence on adults

The pair-correlation function revealed that the juveniles in the plots without disperser showed a tight association with adults with neighbourhood density *c.* 20 times higher density than expected by an independent placement of juveniles; (Fig. 3a). A parameter $2\sigma = 2$ m produced a reasonable fit of the corresponding point process that places juveniles around the observed adult locations (Figs 3a and S9, Supporting information). Testing the fit with the $D(r)$ indicated an overall good fit, but at distances between 1.5 and 9.0 m, the nearest juvenile was for *c.* 10% of all adults somewhat further away than expected by the null model. This was caused by 'isolated' adults with no surrounding juveniles (see Fig. 1).

Unexpectedly, juveniles in the plot with dispersers showed also a strong association with adults, with a neighbourhood density being *c.* 10 times higher than expected by independence (Fig. 3b). However, the absolute neighbourhood density of juveniles in the neighbourhood of adults was 4-to-10 times higher in the presence of disperser (Figs 1 and S10, Supporting information). The point-process model corresponding to the adult dependence hypothesis yielded a good fit of the data, but somewhat underestimated the observed neighbourhood density at distances larger than 6 m (Fig. 3b). Visualizing the data (Fig. 1) suggested that this departure may be caused by a lower juvenile density in the south-western patch not accommodated by this point process.

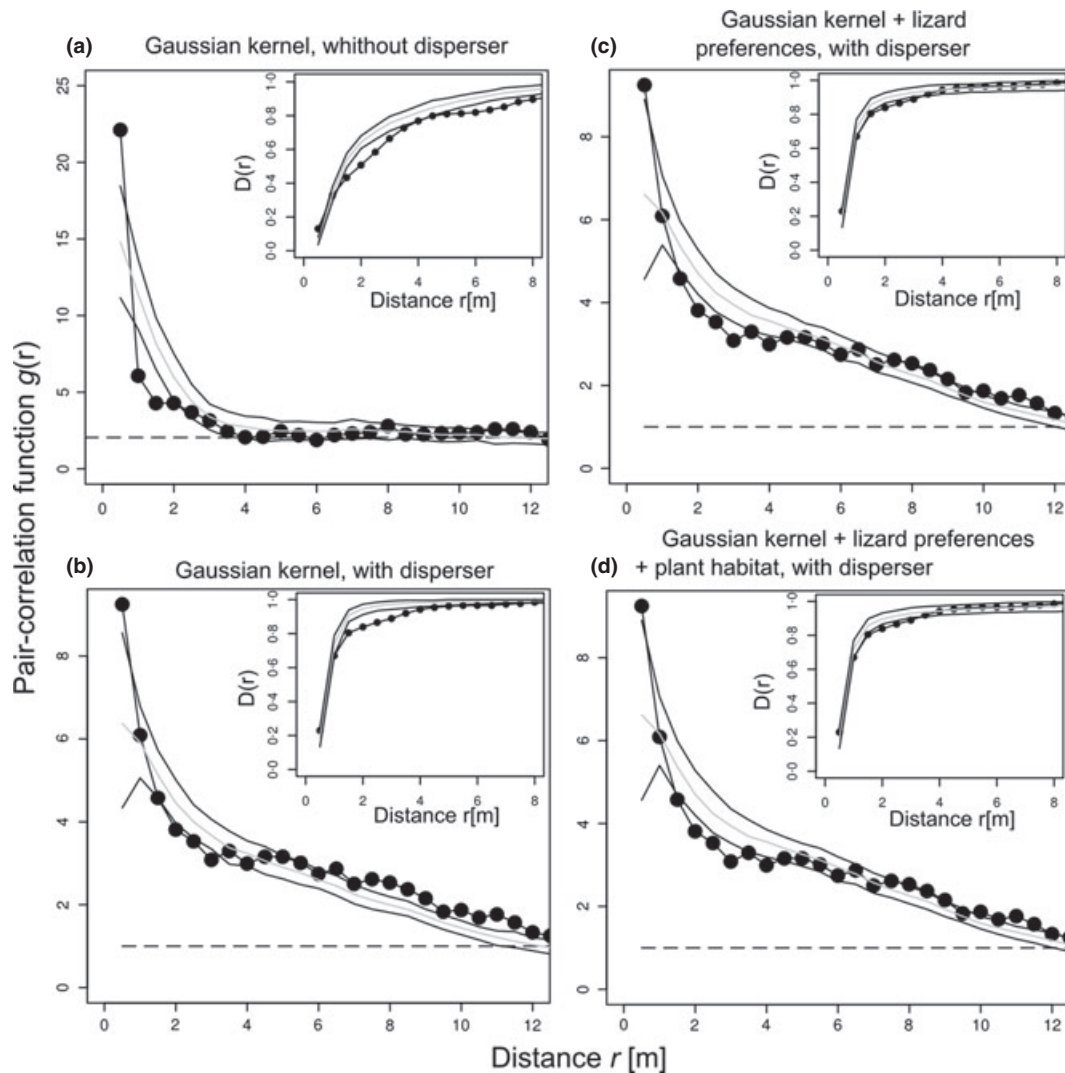


Fig. 3. Analyses of the juvenile–adult relationships. We contrasted the pair-correlation function of the bivariate adult–juvenile patterns to several point-process models that represent the dependence on adults hypothesis (a, b) and the combined hypotheses (c, d). Panel a shows results for the plots without disperser, and panels b and d for the plots with disperser. The point-process models representing the dependence on adults hypothesis distributed juveniles following a Gaussian kernel around the observed locations of adult plants, whereas the combined hypotheses considered additionally the lizard habitat preferences (c) and lizard and plant habitat suitability (d). For further conventions, see Fig. 2.

Dependence on multiple processes

Indeed, the point-process model that combined hypothesis (ii) (lizard activity) and hypothesis (iii) (proximity of adults) improved the fit of the $D(r)$ (cf. insets Fig. 3b,d), but not combining with hypothesis (i) (habitat suitability) (cf. Fig. 3c,d; Appendix S3, Supporting information). Figure S11 (Supporting information) provides additional support for this finding and added that 40% of juveniles lack a juvenile–adult association at the low-density south-western patch (see Appendix S3, Supporting information).

ANALYSIS 3: MORTALITY IN PLOTS WITHOUT DISPERSER

Juvenile survival in the plots without dispersers was lower within the immediate neighbourhood of adults (i.e. <1.5 m; Figs 4 and S9, Supporting information).

Discussion

In this study, we used point-pattern analysis to quantify detailed characteristics of the spatial patterns of the shrub *D. rodriguezii*. This shrub species persists in populations with and without its unique seed disperser, the lizard *P. lilfordi*, which offers a unique opportunity to study how the activity of a disperser affects the spatial distribution of a plant species. To this end, we contrasted the observed patterns to several point-process models that represented our hypotheses on the factors that shape the plant patterns. We found clear results that, however, did not always match our initial expectations.

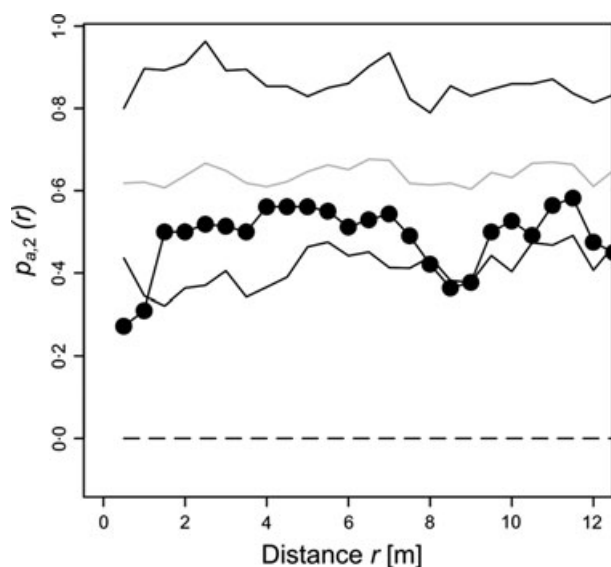


Fig. 4. Influence of the proximity of adults on juvenile survival for plots without disperser. We used the probability of survival $p_{a,2}(r)$ of juveniles at distance r from adults as summary statistic and contrasted it to the random mortality null model for the juveniles. Solid circles were the observed statistic, whereas solid lines showed simulation envelopes of the null model.

In heterogeneous landscapes, an intermediate dispersal distance should allow fast population growth because offspring often end up in the same favourable habitat as the parents, but not too close to them to suffer severe competition (Cousens, Dytham & Law 2008). However, in the absence of a seed disperser, fruits drop and recruit very close to the canopy of adults (e.g. Traveset & Riera 2005). This mechanism can create the observed strong small-scale clustering of juveniles around adults. Seeds deposited below *D. rodriguezii* adults are placed in high-quality habitat, which may yield stable long-term population dynamics characterized by self-replacement (Rodríguez-Pérez & Traveset 2010, 2012). However, unoccupied habitat at intermediate distances from adults cannot be occupied, and the resulting high juvenile densities around the adults (Fig. S10, Supporting information) may yield distance-dependent mortality of juveniles close to adults. In our case, we observed that the neighbourhood density of juveniles at distances beyond 1 m from adults was 4-to-10 times higher when the seed dispersers were present, whereas absolute juvenile densities in the immediate neighbourhood (i.e. ≤ 1 m) of adults were similar in both cases (Fig. S10, Supporting information). This suggests that the lizards may transport seeds to nearby locations of favourable habitat where juveniles escape adult competition (Rodríguez-Pérez & Traveset 2010) and that distance-dependent mortality (mediated by other mechanisms, such as allelopathy or shading) may control juvenile densities in the immediate neighbourhood of adults (Harper 1977).

Independently of the lizard's presence, juveniles were closely aggregated around adults. However, this unexpected result may not necessarily reflect dispersal limitation (Münzbergová & Herben 2005) but rather reflect the underlying disperser activity (Russo & Augspurger 2004; Rodríguez-Pérez, Wiegand & Santamaría 2012). *D. rodriguezii* fruits are quickly consumed by lizards in Colom Islet (Traveset & Riera 2005; Rodríguez-Pérez & Traveset 2010), and lizards can cover several times their home range before seed defecation occurs (Santamaría *et al.* 2007). Consequently, juvenile clustering around adults may not indicate parent–offspring relationship (Hardesty, Hubbell & Bermingham 2006; Sezen, Chazdon & Holsinger 2009), but be caused by dispersers defecating under feeding sites (Julliot 1997; Russo & Augspurger 2004).

Our data also detected that some juveniles in Colom Islet occurred in low densities (i.e. <10% total plants) and were not locally associated with adults (Figs 2 and S11, Supporting information). Consistent with this result, Rodríguez-Pérez, Wiegand & Santamaría (2012) found that <10% of juveniles were located at favourable habitats that showed low lizard activity. The presence of these juveniles might be caused by sporadic excursions of lizards outside their home range. Although this behaviour did not appear to strongly influence the overall spatial patterns studied here, it may guarantee that the plants could eventually arrive (thanks to lizards' activity) at the best spots of habitat, and thus connect high-density clumps of plants.

On the long-term, this may allow *D. rodriguezii* to reach high population numbers such as that observed at the Colom Island.

We found that point-process models that only considered habitat suitability of *D. rodriguezii* were not able to correctly predict the observed spatial patterns. Therefore, the small-scale clustering observed in the plots without disperser should be caused by dispersal limitation but not primarily by fine-scale habitat configuration. Although the presence of nurse plants is a key for the regeneration and plant population dynamics of *D. rodriguezii* (Traveset & Riera 2005; Rodríguez-Pérez & Traveset 2010, 2012), our present results suggest that such habitat is abundant and does not limit the spatial distribution of this endangered plant. Without dispersers, juveniles establish in appropriate spots of habitat (Rodríguez-Pérez & Traveset 2010), but compete with adults (Fig. 4). Disperser activity structures the broad-scale spatial distribution of adults (Fig. 2; Rodríguez-Pérez, Wiegand & Santamaría 2012) and increases the relative juvenile density by transporting some seeds farther away from the adults (Fig. 1 and S11, Supporting information; Rodríguez-Pérez, Wiegand & Santamaría 2012), with ultimately higher chances of plant survival (Fig. 4). Thus, while adult proximity is the dominating factor in explaining the plant pattern, the habitat suitability for disperser home ranges had a smaller but discernible broad-scale impact on plant distribution.

Point-pattern analysis allowed us to derive hypotheses on the mechanisms that shaped the dynamics and spatial pattern of the populations of *D. rodriguezii* with and without seed disperser. However, we cannot fully exclude the possibility that another set of mechanisms may result in similar patterns. To reduce this risk, we analysed different aspects of the spatial patterns (i.e. pattern of juveniles, adults, spatial relationship between juveniles and adults, and juvenile survival in relation to adult proximity; Wiegand *et al.* 2003). In this sense, experimental evidence is required to test our specific hypotheses (Traveset & Riera 2005; Rodríguez-Pérez & Traveset 2010).

Conclusions

Contrary to our expectations, we found that the lack of the seed disperser had only a subtle impact on the spatial pattern of *D. rodriguezii*. Our results suggest that plants may self-replace in both populations with and without disperser at favourable spots of habitat, allowing for stable population dynamics (Rodríguez-Pérez & Traveset 2012). The consequences for plant patterns and demography are high juvenile clustering under adults that may lead to distance- and density-dependent mortality. Although disperser activity released the extreme dispersal limitation of *D. rodriguezii*, our results suggest that they still deposited seeds close to adults by 'shuffling' seeds within populations when defecating at feeding sites. However, the higher neighbourhood density of juveniles at intermediate distances from adults observed in the population with dis-

perser suggests that they moved seeds also to intermediate (>1 m) distances from adults where they escaped adult competition. Additionally, occasional movements of lizards beyond plant clusters may guarantee long-term population connectivity, occupancy of newly emerging favourable sites (Rodríguez-Pérez, Wiegand & Santamaría 2012), and the observed high population numbers (Rodríguez-Pérez & Traveset 2012). Our study showed how detailed analyses of spatial patterns can help to close the gap in the 'demographic loop' that separates observations of limited seed dispersal from the long-term consequences of dispersal in plant populations (Levine & Murrell 2003; Howe & Miriti 2004).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Habitat suitability maps.

Appendix S2. Technical detail on point-process models.

Appendix S3. Additional results of point-pattern analysis.

Table S1. Results of generalized linear model of habitat suitability predicting the presence of adults.

Fig. S1. Environmental categories and spatial location of adult plants in each studied plot.

Fig. S2. Habitat suitability maps derived from model-dependent probabilities of habitat presence.

Fig. S3. Example for a point pattern created by a Thomas process and the associated pair-correlation function.

Fig. S4. Example of an intensity function.

Fig. S5. Example of a Gaussian shadow with parameter $\sigma = 2$ m for the Colom Island plot.

Fig. S6. Univariate analyses (Thomas process) of adult and juvenile plants of *D. rodriguezii* in each plot without disperser.

Fig. S7. Univariate analyses (habitat suitability) of adult and juvenile plants of *D. rodriguezii* for each plot without disperser.

Fig. S8. Univariate analyses of habitat-dependent processes of adult and juvenile plants of *D. rodriguezii* in the plots without and with disperser.

Fig. S9. Analyses of bivariate heterogeneous Poisson process and random mortality of *D. rodriguezii* juveniles for each of the plots without disperser.

Fig. S10. Analysis of bivariate pattern of *D. rodriguezii* juveniles around adults in the plots with and without dispersers.

Fig. S11. Analyses of bivariate heterogeneous Poisson process of *D. rodriguezii* juveniles around adults in the plot with disperser.

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